# Evolving conformity: conditions favouring conformist social learning over random copying

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## Abstract

There is a growing interest in the relative benefits to the learner of the different social learning strategies used to transmit information between conspecifics, and in the extent to which they require input from individual learning. To date, theoretical models have tended to examine the success of particular strategies in relation to specific parameters or circumstances. This study employs individual-based simulations to derive the optimal proportion of individual learning that co-exists with random copying and conformist social learning strategies in populations experiencing wide-ranging variation in levels of environmental change, reproductive turnover, learning error, and individual learning costs. Predictions derived from the literature – that optimal levels of individual learning will be higher for both strategies when the rate of environmental change is higher, and when reproductive turnover and individual learning costs are lower, are supported. Contrary to the theoretical prediction, optimal levels of individual learning are sometimes higher under higher levels of learning error, particularly when reproductive rates are low. Results for the two strategies are qualitatively similar, but demonstrate numerous parameter combinations under which random copying is fitter than conformist social learning. Contrary to established expectations, the strategy employing the lesser proportion of individual learning is not always the fittest.

## Keywords

Social learning; asocial learning; conformity; random copying; reproductive rate; environmental change.

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## 1. Introduction

There is currently considerable interest across a broad range of disciplines in the social learning strategies that facilitate the transmission of information between conspecifics (e.g Aplin et al. 2015a; Muthukrishna et al. 2016; Nakahashi et al. 2012). Such research encompasses the development of theoretical models as well as experimental analyses of numerous species. Two types of social learning strategy are examined in the current paper: random copying, a baseline strategy in which a model is selected from the population at random, and 'conformist' copying, in which there is a disproportionate bias towards selecting a common variant as a model (e.g. Boyd and Richerson 1985; Muthukrisha et al. 2016). Of particular importance is the extent to which populations operating these two strategies will require input from individual learning to facilitate adaptation to changing environments. Traditionally, theory suggests that social learning avoids the costs (in terms of time and risk) associated with individual trial-and-error learning, but that its value decreases as the rate of environmental change increases, as this in turn increases the likelihood that the information learnt will be out of date (e.g. Boyd and Richerson 1985). Following a brief review of the relevant literature on random and conformist social learning strategies, a simulation model is introduced that allows populations operating each of these two strategies to evolve optimal proportions of individual learning, and measures the fitness of these optima under variation in a number of other biologically and culturally relevant parameters.

On a theoretical basis it has been argued (Boyd and Richerson 1985; Henrich and Boyd 1998) that because those variants favoured by natural selection will often exist at the highest frequencies in a pool of potential targets for copying, conformity provides a simple, adaptive social learning rule under a very broad range of conditions. On this view, conformity provides a cheap shortcut that prevents individuals having to monitor the performance of conspecifics, as they would have to if using the various payoff-biased strategies. Other researchers, however, have suggested that conformity may prevent the spread of beneficial innovations, reducing the cultural diversity of the population and hindering cumulative cultural evolution (Henrich and Boyd 1998; Eriksson et al. 2007; Kandler and Laland 2009). The model of Eriksson and colleagues (2007), for example, demonstrates situations in which a random copying strategy allows for more rapid accumulation of adaptive innovations that a conformist strategy. If beneficial innovations occur in the population at low frequency – akin to mutations in the genetic system – then they are likely to be quickly lost in situations where a strong conformist bias exists.

Since variation provides the raw material on which selection acts (e.g. Price 1970, 1972), the homogenising effect of conformity could be highly damaging, particularly in changing environments. A particularly powerful argument concerning the dangers of cultural homogeneity comes from the work of Whitehead and Richerson (2009). These authors modelled the evolution of learning strategies in stochastically fluctuating environments, and found that the low cost of social as opposed to individual learning in their simulations often led to the elimination of the latter. This tended to happen during periods of relatively low environmental variation, when the benefits of individual learning in tracking environmental change were low relative to the costs of the strategy. The resulting dominance of social learning, however, removed the ability of the population to track

subsequent environmental changes. If such changes were relatively large, populations collapsed due to their inability to produce novel behaviours. The work of Whitehead and Richerson (2009) is particularly intriguing in that the environments to which individuals were adapting were characterised by similar frequency spectra to those found in empirical palaeoclimatic datasets (e.g. Ditlevsen et al. 1996). Whitehead and Richerson (2009) further note that the only way in which populations pursuing pure social learning strategies can avoid extinction in their simulations is to switch to a pay-off based, rather than a conformist, social learning strategy. In a similar vein, Kandler and Laland (2013) find that as rates of environmental change increase and conformity becomes less adaptive, the conformist bias must either be weakened or coupled with higher rates of individual learning (see also Efferson et al. 2008).

Finally, the empirical evidence for conformity is weak (e.g. Eriksson et al. 2007), with empirical studies hampered by the need to demonstrate *positive* frequency-dependence. A critical step forward in the empirical study of social learning has been the recognition that a finding of frequency-dependence can imply a process of random copying, whereas a finding of *positive* frequency-dependence is required to infer a process of conformist copying (e.g. McElreath et al. 2008; though see Acerbi et al. 2016). The logic here is that although copying may be random, a copier is more likely to copy a variant that exists in the population at high frequency because she is more likely to be exposed to such a variant (or, equivalently, she will be exposed to such a variant more often). Frequency-dependence is depicted by the blue line in Figure 1; note that frequencies before and after learning are equal (on average) under frequency-dependent copying. The red line in Figure 1 depicts positive frequency-dependence, under which high-frequency variants increase in frequency after learning, with low-frequency variants decreasing. In order to infer a process of conformity, empirical studies must demonstrate a sigmoid curve similar to the red line in Figure 1, with proportions of variants changing due to social learning through time.

Where evidence for conformity appears robust, a simple 'copy the majority' rule provides greatest explanatory power (e.g. Aplin et al. 2015a; Pike and Laland 2010; Morgan et al. 2012). Kandler and Laland (2009:65) argue on theoretical grounds that "strong conformity is unlikely to be widespread in human culture", whilst Eriksson and colleagues (2007) suggest that there is no satisfactory evidence that a conformist bias exists in human social learning. Nonetheless, there remains a conviction, rooted in the human psychology literature of the early twentieth century (e.g. Jenness 1932; Sherif 1936; Asch 1956), that conformity is a powerful force in human social learning. There has also been considerable research into conformity in other species, ranging from primates (e.g. Dindo et al. 2009; Whiten et al. 2005; Hopper et al. 2011; van de Waal et al. 2013) to rats (e.g. Galef and Whiskin 2008), birds (e.g. Rosa et al. 2012; Aplin et al. 2015a), and fish (e.g. Pike and Laland 2010).

Pike and Laland (2010) demonstrated that nine-spined sticklebacks given a choice of two feeders chose the one at which they had witnessed the majority of conspecifics feeding, despite having earlier learnt by experience that the feeder in this position dispensed less food than the other. Crucially, the number of fish choosing to neglect their individually learned preference in favour of copying others increased disproportionately as the size of the majority being copied increased. Aplin and colleagues (2015a) captured wild great tits and trained them to feed from a puzzle box by opening a door with their bill from either the left or the right of the box. Differently trained individuals were then released into different areas, and their conspecifics rapidly learnt from them

how to open the puzzle boxes placed in their habitats. Naive birds in each area copied the solution learned by the trained individuals released there, with subsequent adoption based disproportionately on the local majority strategy. Importantly, even birds exposed to both solutions continued to display the local majority strategy, and of birds that relocated to areas with different strategies, 71% altered their behaviour so as to conform in the new location. These studies are highly persuasive of the presence of conformist social learning, yet an active debate continues as to the presence of possible confounds and the possibility of alternative, more parsimonious explanations (e.g. van Leeuwen and Haun 2014; Aplin et al. 2015b; van Leeuwen et al. 2015, 2016; Acerbi et al. 2016; Whiten and van der Waal 2016).

Random copying, the second strategy examined here, has also received considerable attention from behavioural biologists. Slater and colleagues (1980:210), for example, suggest that different song types among chaffinches are selectively neutral, appearing to "arise and be lost from the population at random, without the transmission of some being favoured over that of others". Similarly, Hahn and Bentley (2003) find that the distribution of baby names in the United States over a 100-year period can be explained by a process analogous to genetic drift, with parents randomly copying names from others. An important element of this pattern is what they refer to as 'proportional sampling'; parents are more likely to be exposed to, and therefore more likely to copy, names that are already popular. This phenomenon, more often referred to as frequency-dependence, is equivalent to random copying; copying is random, but conditioned on the frequency of stimuli that the subject is exposed to. A critical step forward in the empirical study of social learning has been the recognition that a finding of frequency dependence can imply a process of random copying, whereas a finding of *positive* frequency dependence is required to infer a process of conformist copying (e.g. McElreath et al. 2008; though see Acerbi et al. 2016). Finally, in an expansion of the techniques employed by Hahn and Bentley (2003), Herzog and colleagues (2004) demonstrated that the popularity of purebred dogs in the United States over a 50-year period fluctuated in a manner consistent with random copying, though with some identified anomalies.

The above examples reflect situations in which there are no apparent fitness differences between the available variants; as no variant is 'fitter' than any other, choices reflect varied individual motivations and preferences that, when aggregated, appear random at the population scale. Archaeologists have long attempted to divide material culture traits into those that are subject to natural selection and those that have no impact on fitness and are thus likely to vary in frequency in random fashion (e.g. Dunnell 1978; Neiman 1995; Custer 2001; Shennan and Wilkinson 2001; Brantigham 2007). In particular, Dunnell's (1978) distinction between stylistic and functional elements expresses this dichotomy, though it should be noted that stylistic elements often have a social function that may ultimately contribute to an individual's fitness. Archaeological examples of apparently random copying of stylistic traits have been found in studies of Woodland period ceramics from Illinois (Neiman 1995) and decorative band types on pottery from Neolithic settlements in western Germany (Shennan and Wilkinson 2001; Bentley and Shennan 2003).

It is relatively easy to appreciate how fitness-neutral or stylistic traits could come to be copied at random, but harder to imagine a similar mechanism operating on the transmission of fitness-conferring traits. In certain circumstances, however, the latter can indeed occur. Tanaka and colleagues (2009) demonstrate that the maintenance and transmission of various complementary and alternative medical practices between individuals does not depend on the efficacy of those

practices. These authors show that superstitious treatments with no medical benefit, and even maladaptive practices that harm their users, can be retained at relatively high frequencies. Whilst a demonstration that treatments are not copied on the basis of their efficacy alone is not sufficient to demonstrate random copying, the authors also develop a model of random copying that adequately describes the empirical pattern. It appears that in this case individuals attempt to acquire effective treatments, but often fail to do so due to cultural biases and the difficulties of accurately assessing the relative performance of any given treatment (Tanaka et al. 2009). The aggregate pattern that results thus resembles random copying.

There are a number of important reasons for comparing random and conformist copying. Firstly, Tanaka and colleagues (2009:7) make the important point that the assumption of random copying in their model is "simple and parsimonious". Whilst they do not elaborate on this point, random copying can be seen as parsimonious both in terms of time and in terms of the cognitive demands that it places on the learner. Random copying requires the learner to copy only a single conspecific, whereas conformist copying implies the ability to monitor the behaviour of multiple individuals such that the majority behaviour can be accurately discerned. Secondly, random copying is an appropriate baseline condition for the study of all social learning strategies; such 'unbiased' copying is the essential null model against which all other learning strategies should be tested. Finally, since random copying equates to frequency-dependence and conformist copying equates to *positive* frequency-dependence, this comparison is particularly germane; it is not unreasonable to postulate that conformist transmission, where it exists, has evolved from an ancestral pattern of random copying.

The model introduced below employs individual-based simulations to derive the optimal proportion of individual learning that co-exists with random copying and conformist or 'copy the majority' strategies (henceforth CR and CtM) in populations experiencing differing levels of environmental change, reproductive turnover, learning error, and individual learning costs. The model allows for rigorous testing of a number of expectations and hypotheses gleaned from the literature surveyed above (e.g. Boyd and Richerson 1985; Efferson et al. 2008; Lewis and Laland 2012; Nakahashi et al. 2012) under variation in a wider set of parameters than has been employed in any previous single study. Through a distillation of previous results, it is predicted that levels of individual learning will be higher for both strategies when:

- The rate of environmental change is higher;
- Reproductive turnover is lower;
- Learning error is higher;
- Costs of individual learning are lower.

Given the difficulty of identifying conformist transmission in natural systems, an important goal of the model is to identify those conditions under which this strategy is likely to be fitter than random copying. Finally, as the proportions of individual learning and fitness are the two principal outputs produced here, the model also provides an ideal opportunity to test the hypothesis (Kendal et al. 2009) that:

- The fittest social learning strategy will be that which requires the lowest proportion of individual learning under a given set of conditions.

## 2. Methods

An evolutionary individual-based model was developed in which a population evolves the optimal proportion of individual learning under a comprehensive set of parameter combinations; the following model description follows the ODD protocol (Grimm et al. 2010).

- *Purpose.* The main purpose of the model is to examine differences in the proportions of individual learning that evolve in populations whose social learning strategy is either random copying (CR) or a conformist 'copy the majority' strategy (CtM). Populations using these two social learning strategies are simulated separately. Rate of environmental change ($\delta$), learning error ($s$), reproductive rate ($r$), and the cost of individual learning ($c$) are varied systematically to examine their effects on the proportion of individual learning that evolves under the two social learning strategies.

- *Entities, state variables, and scales.* The environment is simulated as a symmetrical sawtooth wave that varies in amplitude between simulations. The entities of the model are asexually reproducing individuals that socially learn via either CR or CtM. Each individual is described by three variables: a behavioural phenotype, a proportion of individual learning, and a fitness score. The proportion of individual learning is the only inherited trait of an individual; the behavioural phenotype is learned anew each iteration and the fitness score is determined by how close the phenotype is to the environmental value in a given iteration. The behavioural phenotype and the environment are measured on the same continuous scale. The behavioural phenotype is updated at the start of each iteration through learning. The proportion of individual learning, $\alpha$, determines the extent to which the individual depends on individual learning as opposed to social learning via either CR or CtM.

  The reproductive rate, $r = \{0.1,0.5,0.9\}$, determines what proportion of the population is replaced each iteration; generations are therefore overlapping in the simulations considered here, with the average lifetime of an individual being $1/r$ iterations. The cost of individual learning, $c = \{01,0.5,0.9\}$, reflects the time taken to independently establish a behaviour and the risk of injury potentially associated with doing so, and is implemented during evaluation of the fitness function (see Reproduction, below). The rate of environmental change, $\delta = [0: 0.05: 1]$, reflects the wide range of environmental conditions encountered by many animals on often relatively short timescales. Finally, learning error, $s = [0: 0.05: 1]$, reflects the fact that learning targets, via either individual or social learning, are unlikely to be perfectly met. Simulations, each of 6,000 iterations, were run separately for the two social learning strategies (CR and CtM), and for each combination of $\delta$, $s$, $r$, and $c$, yielding 7,938 simulated combinations. Each simulation was run with a fixed population size of $n$ = 500 individuals.

- *Process overview and scheduling.* At birth, individuals inherit from their parent a value that determines the proportion of individual learning they will engage in. This value is slightly mutated relative to that of the parent (see 'Mutation' below). A learning error ($s$) applies to both individual and social learning (see 'Learning' below). After learning, the fitness of each individual, $F$, is evaluated according to a Gaussian function that takes into account the cost of individual learning. Reproduction then takes place via fitness-proportionate selection (see

'Reproduction' below), with new individuals inheriting only the (mutated) $\alpha$ values of their parents. Prior to the start of the next iteration, the value of the most common phenotype among the survivors is recorded so that it can act as the target for social learning amongst conformist (CtM) individuals in the next iteration. At the same stage, $n \cdot r$ phenotypes from among the $n - n \cdot r$ survivors are randomly sampled with replacement; each one of these phenotypes will act as a target for social learning for one of the CR individuals in the next iteration. Median values of the proportion of individual learning, $\alpha$, and fitness, $F$, in the population of agents are recorded at the end of each iteration. The above schedule then begins again.

- *Design concepts.* The outputs of the model are the proportions of individual learning, $\alpha$, and fitness, $F$, in populations employing the two social learning strategies (CR and CtM) under various combinations of values of the four input variables $\delta$, $s$, $r$, and $c$. Given these outputs, it can be simply determined which strategy employs more individual learning, and which strategy is fitter, for any combination of the four input variables. Changes in $\alpha$ through time emerge from the combined effects of heredity, mutation, differential survival, and differential reproduction, given the values of the four input variables. Mutation, survival probability, probability of reproduction, and both individual and social learning are affected by stochastic variation. The environment has a constant absolute first derivative (i.e. it changes at a constant rate) during each of the 6,000 iterations of any given simulation; the principal results are therefore given as the median values of $\alpha$ and $F$ in the population over the last 5,000 iterations of the simulation (the first 1,000 iterations are discarded).

- *Initialization.* Simulations were initialized with an environmental value of zero. Initial phenotype values were drawn from a normal distribution with a mean of zero and a standard deviation of 0.05. Initial proportions of individual learning were drawn from a uniform distribution on the interval [0,0.1]; differences in these starting values did not affect the outcomes of the simulations.

- *Input.* The model does not have any external inputs.

- *Submodels*

- *Environment*. The environment is a symmetrical sawtooth wave. This waveform was chosen because it has constant absolute first derivative (i.e. the rate of environmental change is a constant) and because, though simple, it captures the periodicity found in empirical (palaeo)climatic data. The rate of environmental change per iteration ($\delta$) is varied between simulations in increments of 0.05 from 0 to 1 by increasing the amplitude of the wave in increments of 2.5 from 0 to 25. Experiments demonstrated that altering $\delta$ via the period rather than the amplitude of the wave did not affect the results.

- *Learning*. At the start of each iteration, all individuals update their behavioural phenotype via a combination of social and individual learning, as determined by their inherited value of $\alpha$. Each individual $i$ learns a behavioural phenotype, $P_i$, in iteration $t$ as

$$P_i(t) = \alpha_i \cdot \beta_i(t) + (1 - \alpha_i) \cdot \gamma_j(t - 1) \quad [1]$$

Where $\alpha$ is the proportion of individual learning, $\beta$ is a value obtained via individual learning and $\gamma$ is a value obtained via social learning, with the subscript $j = \{r, m\}$ indicating the social learning strategy followed (either CR or CtM). An individual aiming for a given target, through either social or individual learning, will achieve a result drawn from a normal distribution with that target as its mean and the learning error value, $s$, as its standard deviation. The target for individual learning is the environment in the current iteration, $w(t)$, whereas the target for social learning is the majority phenotypic value from the previous iteration (CtM) or a randomly sampled phenotype from the previous iteration (CR).

- *Reproduction*. The fitness of each individual, $F_i$, is evaluated according to a Gaussian function with a mean equal to the current environmental value, $w(t)$, and unit variance,

$$(F_i|w(t), P_i) = (1 - c\alpha_i) \cdot \exp(-0.5(w(t) - P_i)^2) \quad [2]$$

  where $c$ is the cost of individual learning. Simulations are run with $c = \{0.1, 0.5, 0.9\}$. The least fit $n \cdot r$ individuals are then removed from the population and replaced by $n \cdot r$ offspring of individuals chosen by fitness-proportionate selection from among the $n - n \cdot r$ survivors, where $n = 500$ is population size and $r = \{0.1, 0.5, 0.9\}$ is the proportion of the population replaced each iteration. New individuals inherit only the (mutated) $\alpha$ values of their parents.

- *Mutation*. Offspring inherit a value determining the proportion of individual learning they engage in; however, this value undergoes mutation as it is transmitted from parent to offspring. Mutation is carried out via a multiplicative lognormal operator of the form $\alpha' = \alpha \cdot \exp(\lambda)$, where $\alpha'$ is the value of $\alpha$ after mutation and $\lambda$ is a value called from a normal distribution with mean zero and a standard deviation of 0.05. The lognormal operator ensures that the proportion of individual learning can never be <0; to ensure that it is never >1, mutated values that are >1 are reset to equal 1.

- *Targets for social learning*. At the end of each iteration the value of the most common phenotype and a random sample with replacement of $n \cdot r$ phenotypes from the parent population are recorded; these values are used as the targets of social learning in the next iteration for the CtM and CR strategies respectively. The most common phenotype is necessarily calculated via a binning procedure: as phenotypic values are recorded at high precision a simple calculation of the modal value is insufficient, as it is unlikely (even in large populations) that any two individuals' phenotypic values will be exactly the same. Surviving phenotypes are therefore assigned to $\lceil (n - n \cdot r)^{0.5} \rceil$ bins of equal width covering the range of values in a given iteration (following Scott 1979); the most common phenotypic value is considered to occur at the mid-point of the bin containing the greatest number of phenotypes.

The model was implemented in Matlab R2017a (MathWorks, Inc., Natick, MA); model code is included as supplementary file CSR_SM4_Model_Code.txt, and figure construction code as supplementary files CSR_SM1_FigType1.txt, CSR_SM2_FigType2.txt, and CSR_SM3_FigType3.txt.

## 3. Results

Results are reported below for evolved proportions of individual learning, and for the fitness of the resulting optima; each subsection begins with a report of trends common to both strategies before proceeding to report important differences between them.

## 3.1. Proportions of individual learning

### *3.1.1. General trends*

As predicted, the evolved level of individual learning is higher in situations in which the rate of environmental change is higher. This can be seen from plots of the proportion of individual learning that evolves under the various conditions considered, provided here for random copying in Figure 2 and for conformist copying in Figure 3. As one would expect, individual learning declines as its cost increases. Increases in the cost of individual learning, however, lead to only quantitative changes; in a given column of figures, each figure above depicts a magnification of the lowest part of the figure below it. This suggests that the *existence* of a greater cost to individual than social learning is more important than the *magnitude* of that cost in producing general patterns in the model.

As predicted, higher rates of reproduction lead to lower levels of individual learning, as demonstrated in Figures 2 and 3. An interesting trade-off emerges, however, between reproductive rate and learning error. At high reproductive rates ($r$ = 0.9), a high learning error leads to a reduction in individual learning; at low reproductive rates ($r$ = 0.1), by contrast, a high learning error can lead to an *increase* in individual learning, provided the rate of environmental change is sufficiently low. This partially conflicts with the basic theoretical prediction that levels of individual learning will be higher when learning error is lower, and is therefore discussed further below.

### *3.1.2. Comparisons between strategies*

In general, Figures 2 and 3 appear very similar, with proportions of individual learning not differing considerably between the two strategies. On closer inspection, however, higher levels of individual learning evolve under random copying in a broad region around the positive diagonal (indicating equality of environmental change and learning error) when reproductive rates are low, under almost all conditions when reproductive rates are intermediate, and when learning error is lower than the rate of environmental change when reproductive rates are high. This can be seen from Figure 4, which facilitates comparison by providing a simple dichotomous representation, with cells coloured black when random copying evolves a higher proportion of individual learning, and white otherwise. Again, it is clear that the cost of individual learning makes only minor differences to the outcome, with these differences having most effect when reproductive rates are low. The 'chequerboard' effect, seen for example in the upper left regions of all three plots under high reproductive rates, demonstrates that differences between the levels of individual learning under the two strategies are marginal, representing merely stochastic variation. It is only with low reproductive rates that considerable regions of the plots show higher levels of individual learning evolving under conformist transmission. At low costs of individual learning these appear primarily where learning error is high relative to environmental change; when learning costs are high, however, such regions also appear where learning error is *low* relative to environmental change.

## 3.2. Fitness

### *3.2.1. General trends*

As predicted, higher fitness occurs at lower learning costs for both strategies, as can be seen for random copying in Figure 5 and for conformist copying in Figure 6. Fitness declines as the rate of environmental change increases; highest fitness occurs in all cases when environmental change is very low and learning error is low to moderate. Regions of high fitness are larger under higher reproductive rates in all cases, and a line demarcating a sharp distinction between regions of high and low fitness is clear, particularly when both reproductive rates and costs of individual learning are high. This line depicts a positive relationship between environmental change and learning error, though the slope of the line varies, being lower at higher reproductive rates.

*3.2.2. Comparisons between strategies*

Overall, higher levels of fitness evolve under conformity when learning error is lower than the rate of environmental change when reproductive rates are low, under almost all conditions when reproductive rates are intermediate, and in a broad region around the positive diagonal (indicating equality of environmental change and learning error) when reproductive rates are high. This can be seen from Figure 7, which provides a comparison of the results of Figures 5 and 6, with cells coloured black when random copying is fitter, and white otherwise.

The regions in which random copying is fitter are affected more by reproductive rate than by the costs of individual learning. When reproductive rate is low, random copying is fitter only in a region where learning error is higher than the rate of environmental change, with the size of this region declining as the cost of individual learning increases. Under moderate reproductive rates, a minimal region in which random copying is fitter occurs when learning error is *much* higher than the rate of environmental change. Random copying is also fitter in a very small region in which learning error is very low and environmental change is moderate to high, a pattern expanded under high reproductive rates. At high reproductive rates there are two clearly demarked regions in which random copying is fitter: these occur (1) when learning error is considerably higher than the rate of environmental change, and (2) when learning error is considerably lower than the rate of environmental change.

Taken in conjunction with the results for individual learning, above, these results demonstrate a very broad accordance with the proposal of Kendal and colleagues (2009) that the fittest strategy will be that which can persist with the lowest proportion of individual learning. To examine this proposal in more detail, Figure 8 shows a plot in which cells are coloured:

- Black if both individual learning and fitness are higher under conformist learning;
- Red if individual learning is higher and fitness is lower under conformist learning;
- Green if individual learning is lower and fitness is higher under conformist learning, and;
- White if both individual learning and fitness are lower under conformist learning.

In this situation, cells coloured green and red are in agreement with the conjecture of Kendal and colleagues (2009), whilst cells coloured white and black oppose this conjecture. As can be seen from Figure 8, there are several regions in which black and white cells appear, suggesting that this conjecture is not supported under all conditions. If ‘chequerboard’ regions are disregarded, white cells appear primarily at low reproductive rates, particularly when rates of environmental change are high relative to learning error; this pattern is particularly pronounced under higher costs of individual learning. Black cells appear primarily in the same regions, but at high reproductive rates.

This suggests that at low reproductive rates random copying strategies can be fitter despite employing a greater proportion of individual learning, whilst at high reproductive rates conformist strategies can be fitter despite higher levels of individual learning.

## 4. Discussion

The key to explaining the patterns of Figure 8 lies first in noting that the cost of individual learning is a model parameter; it is therefore equal for both strategies in any given comparison. The *benefits* of individual learning, therefore, must differ between strategies in those cells coloured either black or white in Figure 8. Both white regions (at low reproductive rates) and black regions (at high reproductive rates) are immediately adjacent to red regions in which individual learning is higher but fitness is lower under conformity. The transition from red to white therefore represents a change in relative proportions of individual learning between the two strategies, whilst the transition from red to black represents a change in relative fitness between the two strategies. A possible explanation for this pattern is that individual learning with error rates lower than rates of environmental change is more beneficial to random copiers at low reproductive rates because it enables them to better track the environment. Conversely, a similar situation under high reproductive rates is more beneficial to conformists because it allows them to maintain variation in their populations.

It should be reiterated that the comparison made in these simulations is between random copying and *strict* conformity (i.e. 'copy the most common variant'). A benefit of random copying is that it is more likely to maintain variation in the population than is conformity. Strict conformity will automatically purge the population of rare innovations due simply to their rarity, even in cases where those innovations are beneficial. More broadly, the more 'positive' positive frequency-dependence becomes, the more likely it will be to remove innovations, which by definition appear at low frequencies. At high reproductive rates, therefore, there is a very real possibility of a conformist population becoming dangerously homogenous, and individual learning is required to maintain variation (see Whitehead and Richerson 2009). This is likely to explain why individual learning is more beneficial to conformists in the black areas of Figure 8.

By contrast, a considerable cost of random copying is that it has only a weak ability to track environmental change. Boyd and Richerson (1985) suggested that conformity could provide a means of tracking environmental change because natural selection will ensure that the commonest variants in the population are also the most common. Random copying, which is ultimately equivalent to frequency-dependent copying, will lead to a qualitatively similar but much weaker result, meaning that individual learning has an important effect in allowing random copiers to track a changing environment. The need for individual learning at low reproductive rates will be particularly pressing for random copiers, since the effects of natural selection in tracking environmental change – which are already weak compared to those for conformists - will become even less effective. This potentially explains why individual learning is more beneficial to random copiers in the white regions of Figure 8. Overall, the hypothesis of Kendal and colleagues (2009) – which is intuitively appealing – requires further testing that considers both the benefits and the costs of individual learning, and how these might differ between different social learning strategies in a given set of circumstances.

Of the generic predictions made above (Section 1) regarding levels of individual learning, most are supported: levels of individual learning are higher when rates of environmental change are higher, and when reproductive rates and the costs of individual learning are lower. The prediction that

levels of individual learning would be higher when learning error is lower, however, was partially contradicted. At low reproductive rates, levels of individual learning were found to be higher under higher levels of learning error. This result is explained by the fact that learning error is the same for both social and individual learners in the model, and that, contrary to established theory, high error rates can sometimes be more detrimental to social learners than individual learners.

Under individual learning, the target for learning is the value of the environment in the current iteration – the same value against which fitness will be assessed. Increasing the learning error is therefore always detrimental to individual learners, as it can only result in phenotypes that are on average further from this optimum. The learning target for social learners is the phenotype of a surviving member of the population, who may already be some distance from the optimum due to environmental change. As learning error is represented as a univariate, Gaussian distribution centred on this learning target, on average half the variation it creates will be in the 'wrong' direction, and therefore half of social learners will acquire phenotypes that are less fit than those of their targets. When learning error is high relative to the rate of environmental change, however, there will also be a proportion of social learners who acquire phenotypes that are too far in the 'correct' direction, and are also therefore less fit than those of their targets. This situation is depicted in Figure 9a. Assuming that the target being copied by a social learner achieved exactly the optimum during the previous iteration, the probability of learning error $s$ resulting in a phenotype that is *better* than the target of social learning under rate of environmental change $\delta$ is given by use of the normal cumulative density function

$$\mathrm{Prob}(P_i^+|s,\delta) = \left[\frac{1}{s\sqrt{2\pi}}\int_{-\infty}^{2\delta} e^{\frac{-t^2}{2s^2}}\,dt\right] - 0.5 \qquad [3]$$

This function is plotted over the range of $s$ and $\delta$ used in the simulations in Figure 9b. Note that this probability declines to very low levels for $s \gg \delta$, leading to a compensatory increase in individual learning when this situation pertains in populations with low reproductive rates. At high reproductive rates, by contrast, natural selection is far more able to capitalise on the phenotypic variance created by high learning error, reproducing multiple copies of variants that happen to achieve high fitness and discarding the remainder.

Having explored the results presented above, it is important here to consider the limitations of the model, including the effects of relaxing the assumptions made, as well as to highlight possible modifications and extensions. As the model presented here parameterises a greater number of variables it necessarily makes fewer assumptions than previous models, but it remains important to consider the effects of those assumptions. In particular, the paragraphs below consider the assumptions that learning errors are equal for social and individual learners and that different social learning strategies entail the same costs; the wider applicability of results gained from the use of a simple model environment and the possible effects of relaxing the assumption of strict conformity are also considered.

A number of possible extensions relate to the assumed structure of costs imposed on the individuals in the model. Whilst the model varies the cost of individual learning, and ensures that it is always higher than that for social learning, it assumes that the learning error is identical for individual and social learning. This is the most sensible baseline assumption, but it may be that social learning, as the 'cheaper' means of modifying behaviour, has been optimised in different ways, and has in fact

been subject to different selective pressures, than individual learning. This will depend on the nature of the social system, the availability of opportunities for social learning, and the ease with which behavioural modification can be achieved via this route. It may be useful in future work to parameterize individual and social learning errors as separate variables, provided this can be done via recourse to empirical findings.

Further to this, there is a logical argument for suggesting that the social learning strategies themselves may entail different costs. Boyd and Richerson (1985), for example, suggest that conformity is a relatively cheap strategy in that it requires learners to monitor only the prevalence of behaviours in the population rather than the success of those behaviours. This logic was designed to show a possible benefit of conformist social learning over a payoff-based strategy, but the logic can be further extended to cover random copying. The costs of monitoring conspecifics are likely to be of two kinds: the time invested, which could otherwise have been utilised performing alternative activities, and the cognitive demands of keeping track of either the prevalence of the success of various behaviours at the group or population level. Both types of cost are minimised by random copying: a model is selected at random, based perhaps on proximity or simply on exposure, and there is no need to monitor individuals beyond the selected model. We might therefore reasonably posit that, in terms of strategy costs, random < conformist < payoff-based. If this scheme is accurate, it would suggest that the results presented above are conservative with respect to the conditions under which random copying is favoured, since neither the time nor the cognitive costs feature in the model.

To ensure results are relatively easy to interpret in relation to rates of environmental change, the model presented here assumes a simple saw-tooth environment with a constant absolute first derivative (i.e. a constant rate of environmental change per iteration). Although this represents an increase in realism over some previous models, such an environment is of course unlikely to occur in nature, and it will therefore be important to consider the effects of more realistically varying environments in future studies. It is suggested here, however, that the mean of the rate of change may be a key variable determining both the optimal balance of individual and social learning and the relative fitness of the various social learning strategies available. The mean rate of environmental change is easily calculated from any quantifiable empirical time series, allowing empirical data to be directly related to the theoretical results presented above. Further theoretical investigations are required, however, as by analogy with palaeoclimatic studies (e.g. Grove 2014, 2017) both the variance of the rate of change and the autocorrelation of the time series may also affect selection on learning strategies. A promising avenue for research in this area is provided by Whitehead (2007; see also Whitehead and Richerson 2009), who uses coloured noises in the white to red spectrum as model environments. As coloured noises have an easily explicable autocorrelation structure, closely approximate real palaeoclimatic time series, and can be scaled to have equal means and variances, they offer condiserable promise as synthetic environments for future models of the kind presented above (Grove in prep).

Finally, it would be useful in future applications of the above model to relax the assumption of strict conformity. Kandler and Laland (2013), for example, found a positive relationship between the strength of conformity and the proportion of individual learning required. This is an intriguing conclusion, suggesting that conformity may only be a dominant strategy when it is relatively weak (i.e. when positive frequency-dependence is only moderately positive). Since weak conformity is a

strategy on the spectrum between random copying and strict conformity, this result has a direct bearing on the model presented above. As discussed above, strict conformity can eliminate beneficial innovations, whereas random copying can fail to adequately track a changing environment. Weak conformity may therefore achieve and optimal balance between these two endpoints, and a useful modelling enterprise would involve allowing the strength of conformity itself to evolve in a model similar that implemented above.

## 5. Conclusions

The model developed above allows populations to evolve optimal levels of individual learning under variation in rate of environmental change, learning error, reproductive rate, and the costs of individual learning, and records the fitness achieved at these optima. This enabled comparison of results for two social learning strategies: random copying, and conformist copying. Predictions derived from the literature – that levels of individual learning will be higher for both strategies when the rate of environmental change is higher, and when reproductive turnover and individual learning costs are lower, were supported for both strategies. Contrary to the theoretical prediction, evolved levels of individual learning were sometimes higher under higher learning errors, particularly when reproductive rates were low. This demonstrates that situations exist in which high learning error is more detrimental to social learning than to individual learning. Results for both proportions of individual learning and fitness for the two strategies were qualitatively similar, and demonstrated a number of regions in which random copying was the fitter strategy. Contrary to expectations, the strategy employing the lesser proportion of individual learning was not always the fittest, suggesting that the benefits of individual learning differ for the two strategies under particular sets of circumstances.

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**Figures**

**Figure 1**. The distinction between frequency-dependence (FD, blue line) and positive frequency-dependence (Positive FD, red line). FD is indicative of random copying, whereas Positive FD is indicative of conformist social learning. Note that only under Positive FD do changes in the proportions of variants occur during social learning.

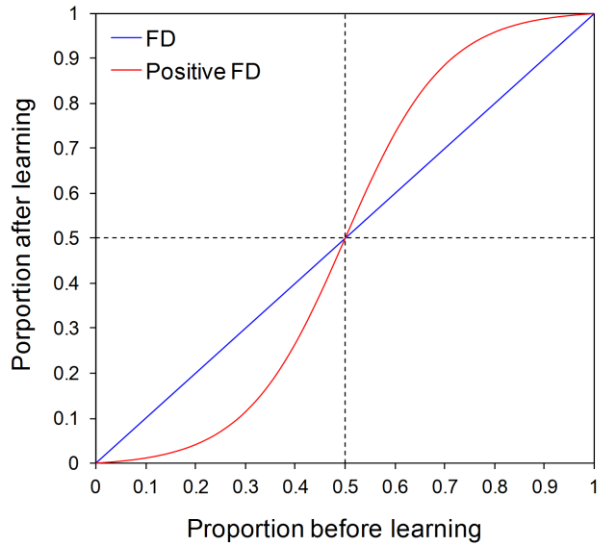


**Figure 2**. Evolved proportions of individual learning in conjunction with a random copying strategy under variation in rate of environmental change, learning error, reproductive rate and cost of individual learning. Note that the single colourbar indexes values in all nine plots.

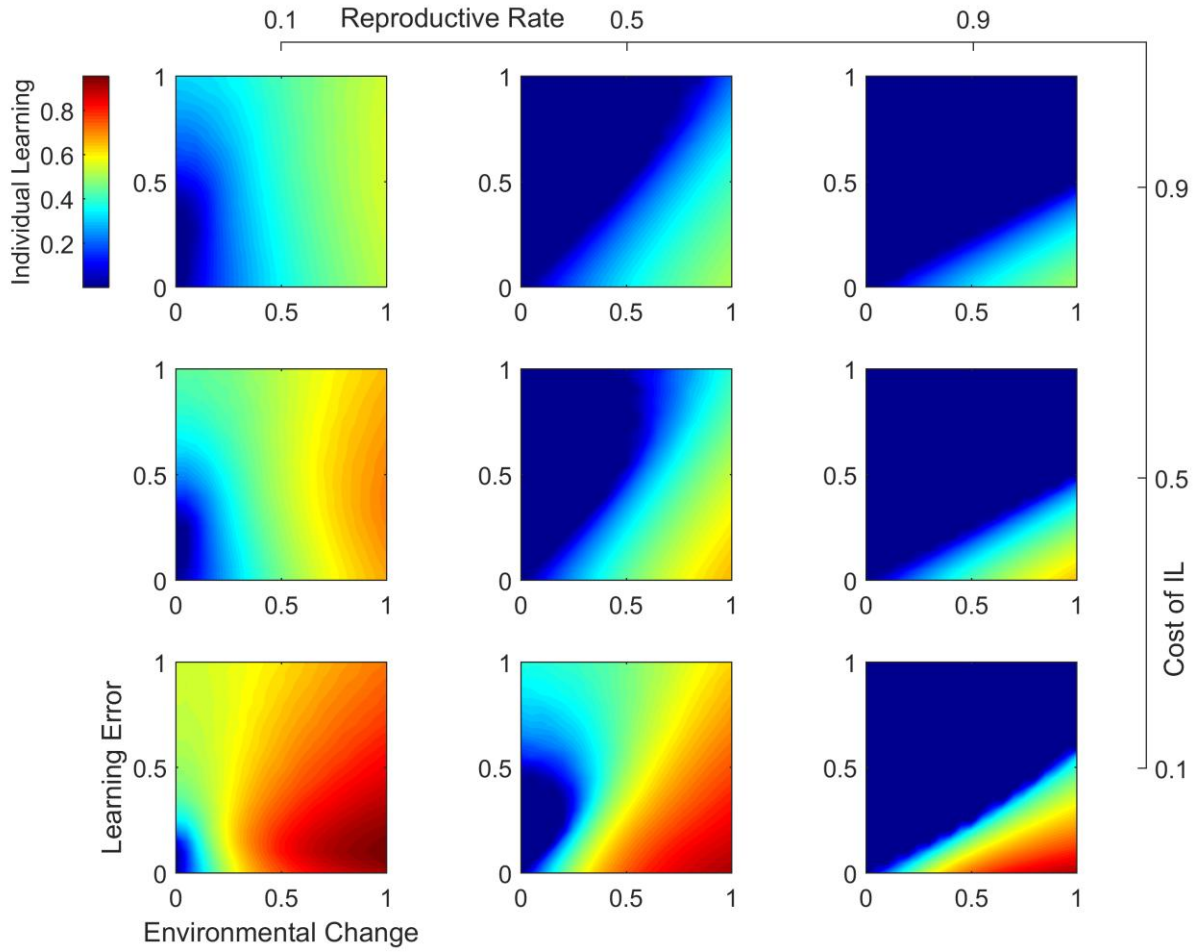
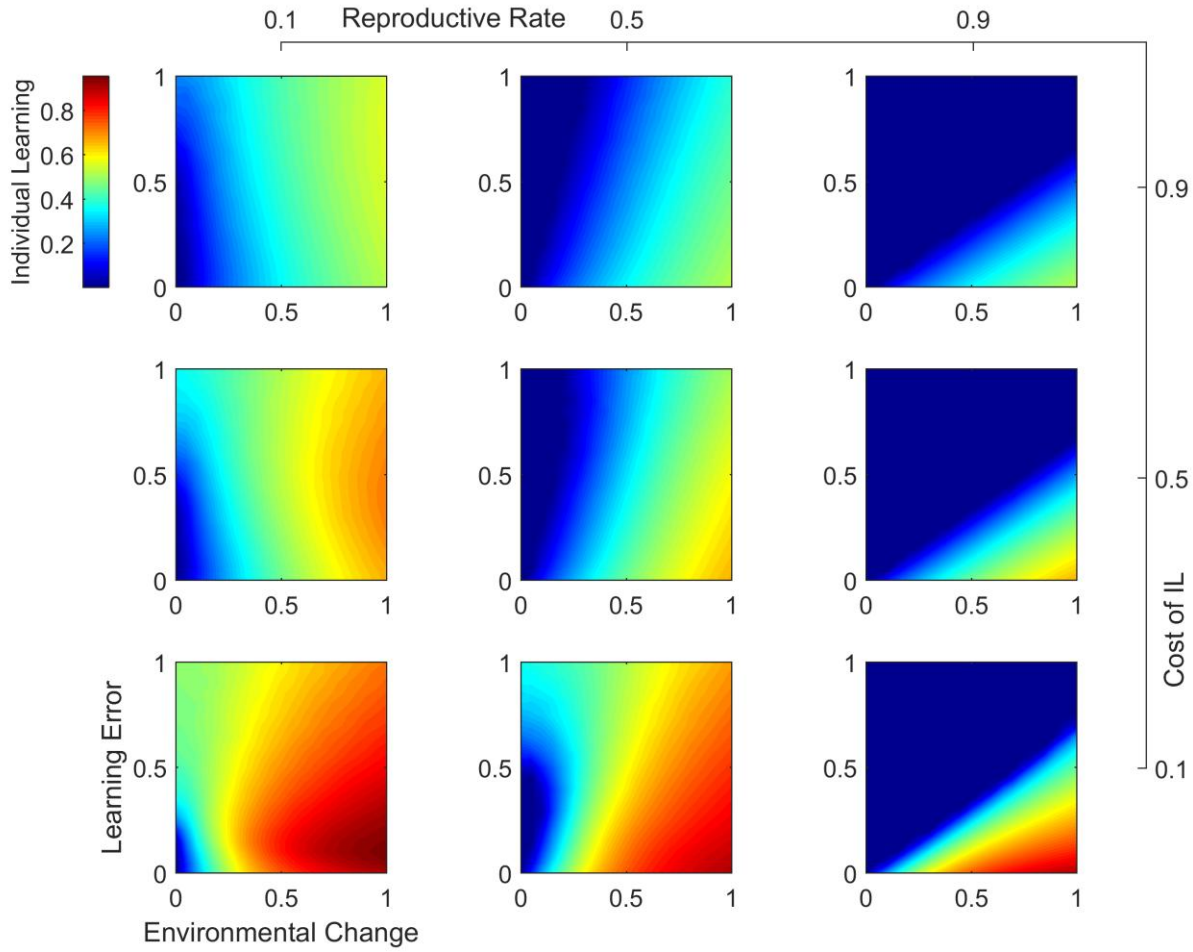


**Figure 3**. Evolved proportions of individual learning in conjunction with a conformist copying strategy under variation in rate of environmental change, learning error, reproductive rate and cost of individual learning. Note that the single colourbar indexes values in all nine plots.



745 **Figure 4**. Comparison of evolved proportions of individual learning under random and conformist
746 strategies. Cells are coloured back if random copying results in a greater proportion of individual
747 learning than conformist copying, and white otherwise.

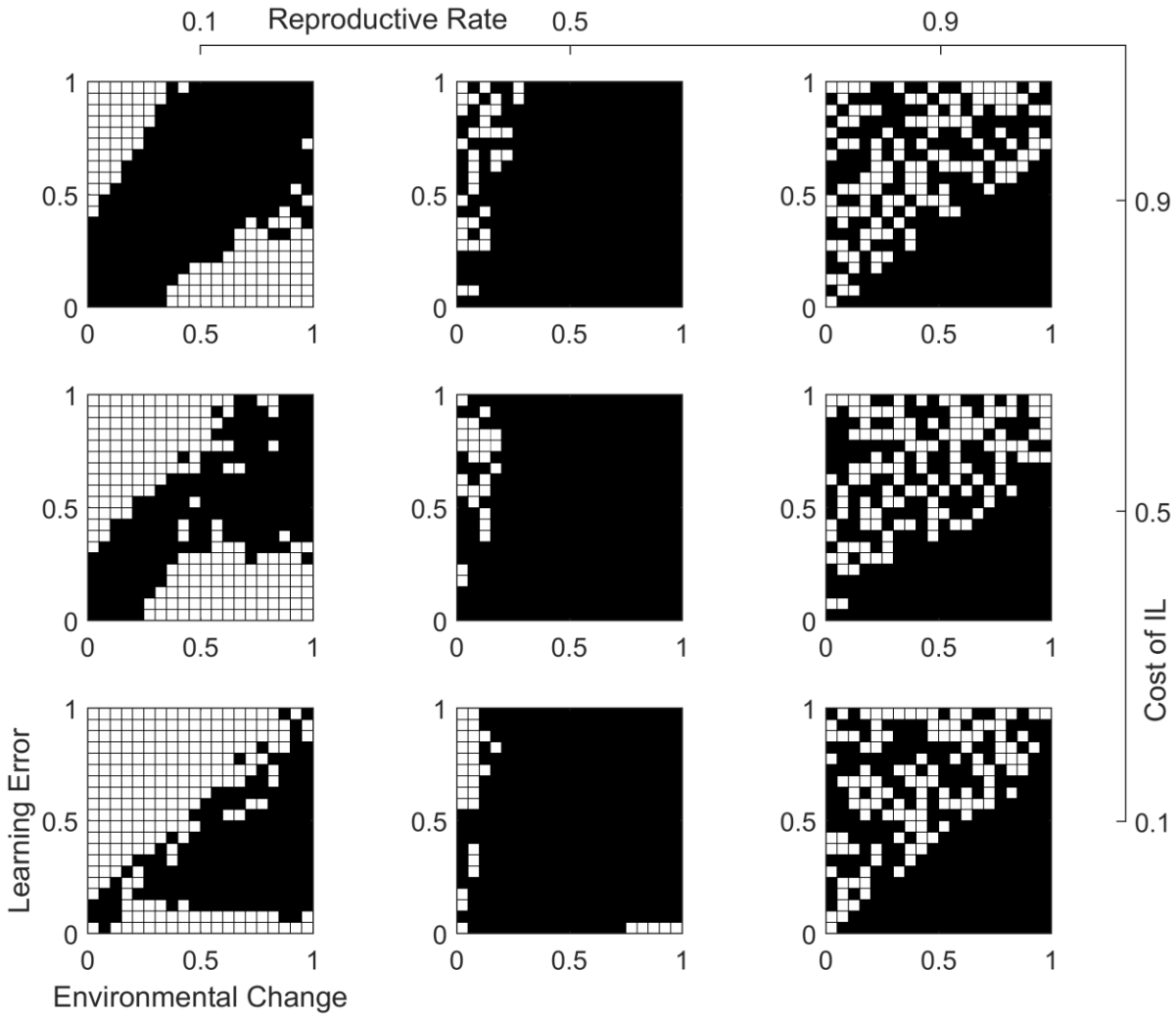



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**Figure 5**. Fitness of the random copying strategy under variation in rate of environmental change, learning error, reproductive rate and cost of individual learning. Note that the single colourbar indexes values in all nine plots.

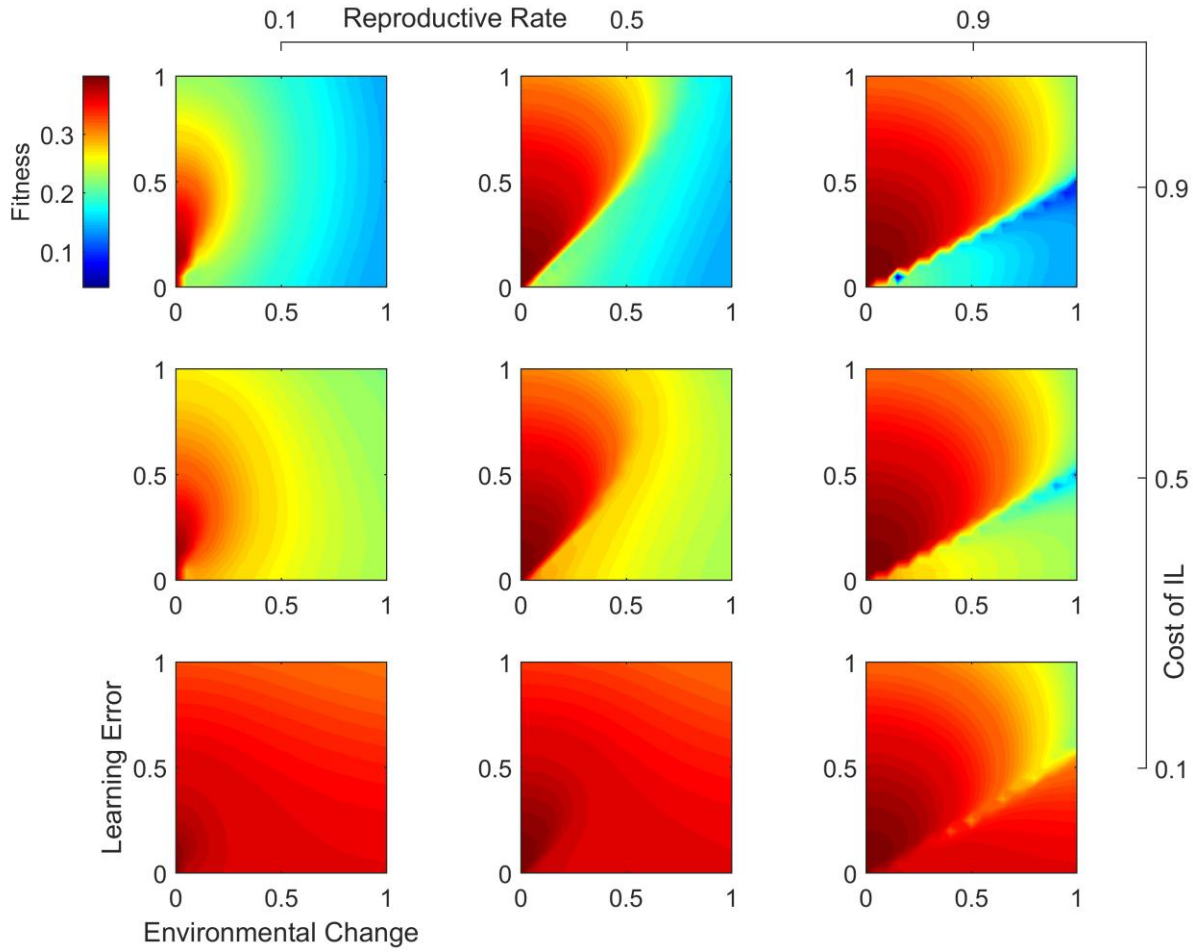

**Figure 6**. Fitness of the conformist copying strategy under variation in rate of environmental change, learning error, reproductive rate and cost of individual learning. Note that the single colourbar indexes values in all nine plots.

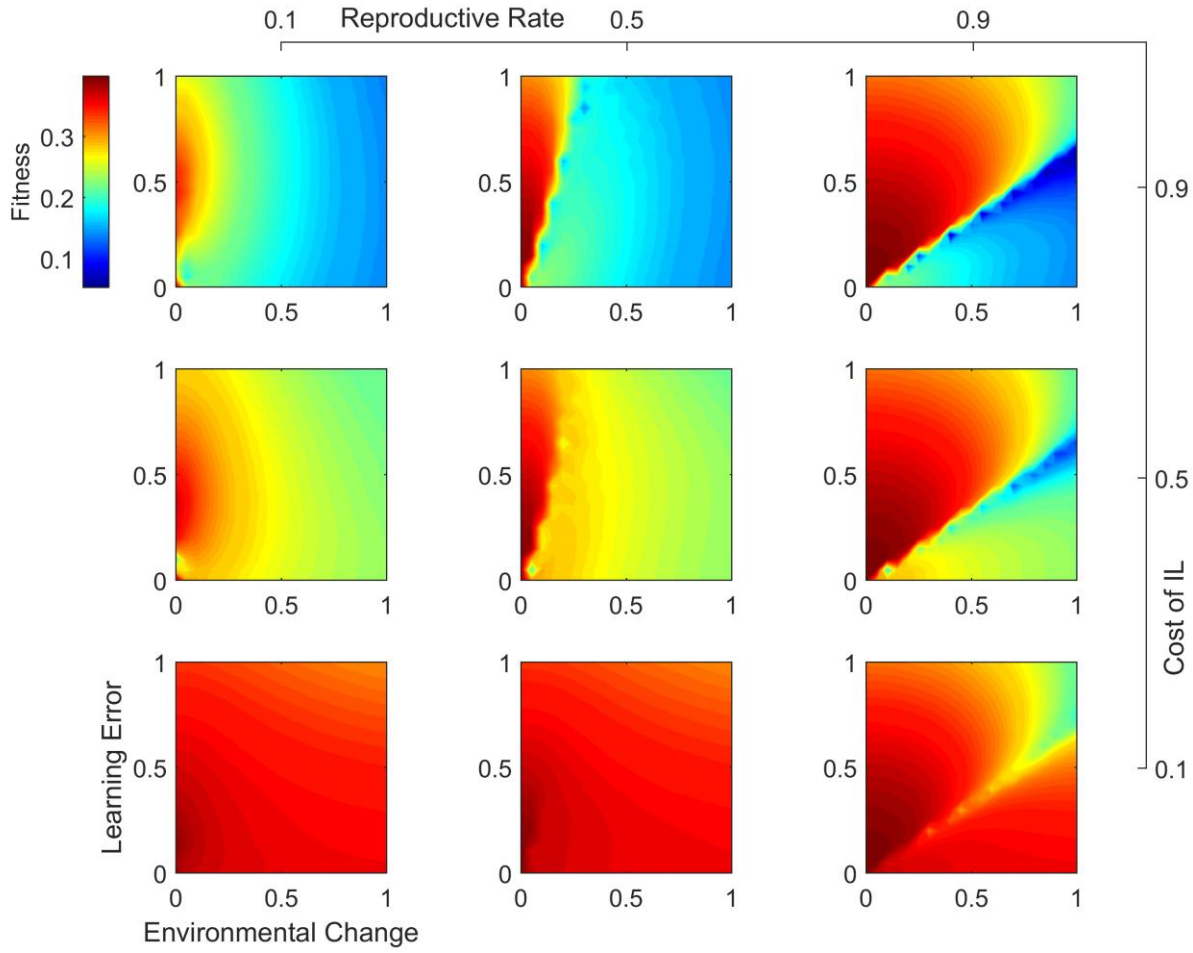

**Figure 7**. Comparison of fitness under random and conformist strategies. Cells are coloured back if random copying results in higher fitness than conformist copying, and white otherwise.

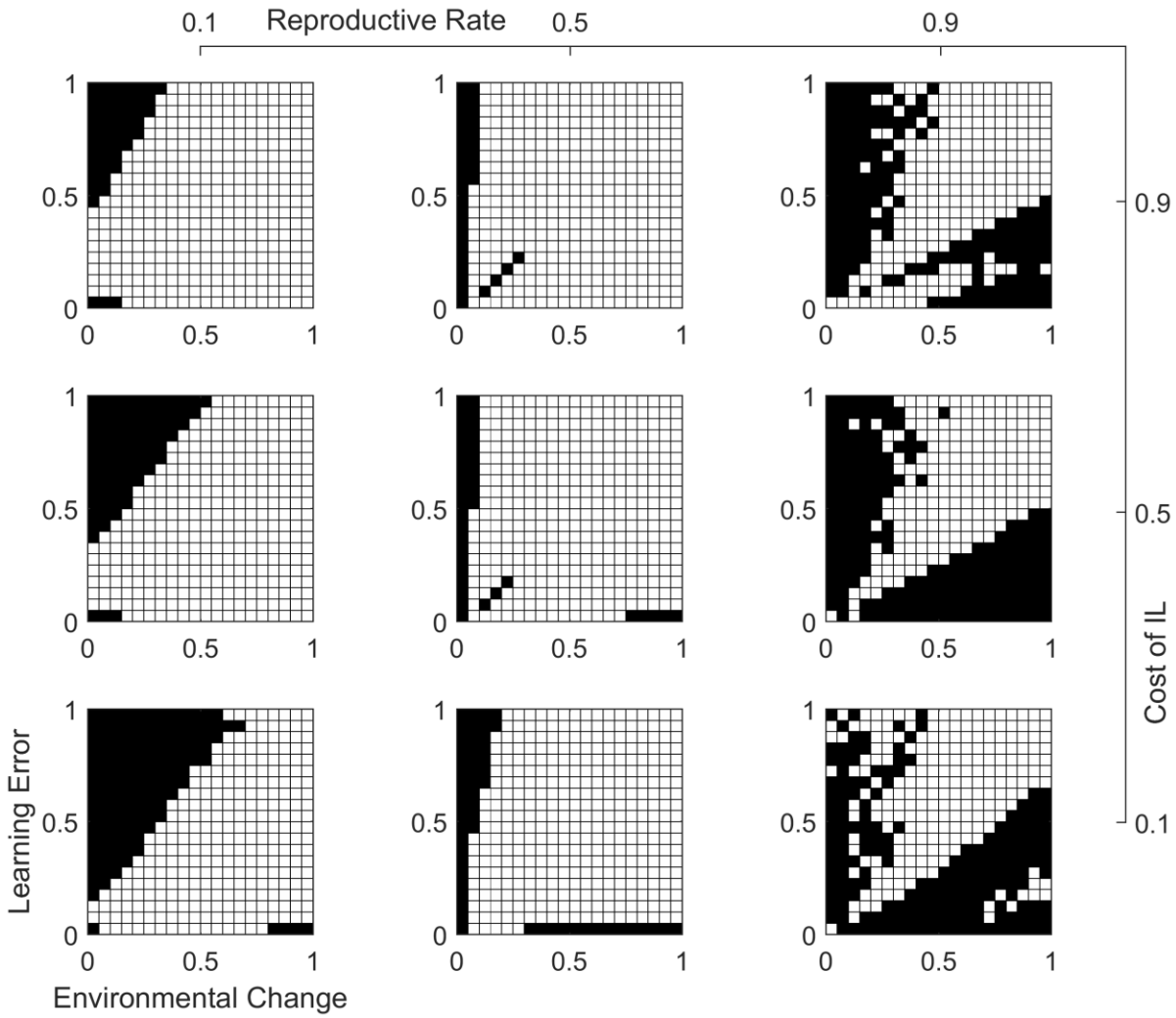

**Figure 8**. Joint comparison of proportion of individual learning (IL) and fitness (F) under random and conformist strategies. Cells are coloured: back if both IL and F are higher under conformity; red if IL is higher and F is lower under conformity; green if IL is lower and F is higher under conformity; white if both IL and F are lower under conformity.

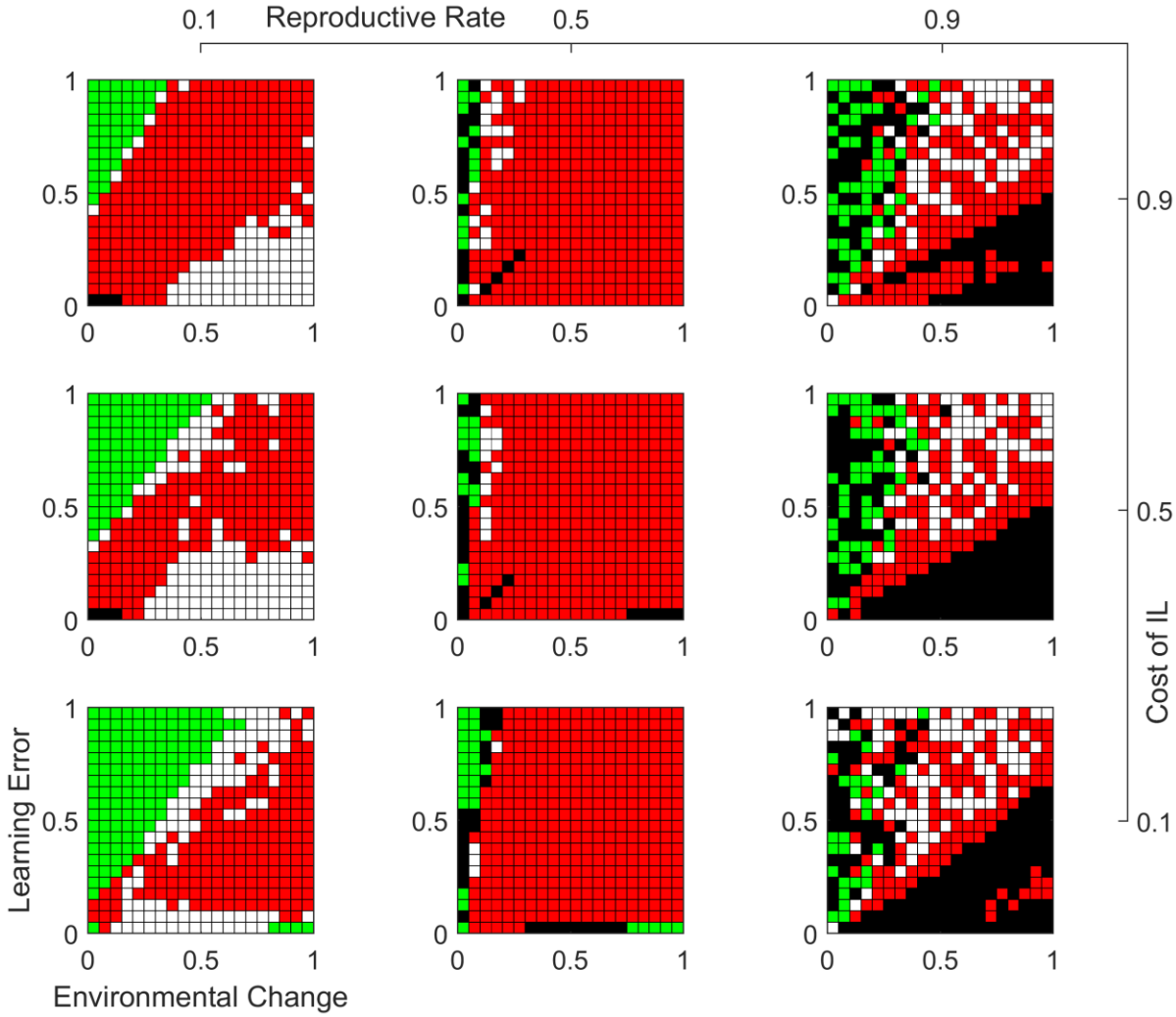

**Figure 9**. Effects of learning error on social learning. a) the target of social learning is at 0, but the environment has since changed by an amount $\delta$. Given a learning error which is high relative to $\delta$, learning error creates two situations in which the copy of the target can be further from the current environment than is the target itself (shaded regions). Half the copies will have moved in the 'wrong' direction, whilst a small proportion will have moved too far in the 'correct' direction (i.e. beyond $2\delta$). a) a rendering of equation [3] over the parameter values of environmental change and learning error used in the simulations, demonstrating that the probability of achieving a copy that is better than the target for social learning is lowest when environmental change is low and learning error is high.